MADROÑO, Vol. 57, No. 2, pp. 129–135, 2010

A RESURRECTION FOR SISKIYOU BELLS, *PROSARTES PARVIFOLIA* (LILIACEAE), A RARE SISKIYOU MOUNTAINS ENDEMIC

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ABSTRACT

We conducted a study of *Prosartes parvifolia* S. Watson, a rare Siskiyou Mountains endemic, currently known from only 15 sites in Del Norte Co., California, and Curry and Josephine counties, Oregon. We found that *P. parvifolia* is (a) fertile, (b) probably not of hybrid origin, and (c) distinct and worthy of recognition as a species. Unlike congeners, its flowers produce ovaries with a single locule, and are pollinated by bees that buzz pollen from connivent anthers. Nectar is not produced. We provide an expanded description, illustrations, and distribution map for *P. parvifolia* as well as a key to the *Prosartes* of northwestern California and southwestern Oregon.

Key Words: Liliaceae, *Prosartes parvifolia*, rare plant, Siskiyou Mountains.

Prosartes D. Don is small genus of North American reticulate-veined Liliaceae formerly treated as part of the Asian genus *Disporum* (Jones 1951; Utech et al. 1995). Sereno Watson (1880) described *P. parvifolia* S. Watson, a species with small campanulate flowers from the Siskiyou Mountains. Although Howell (1903), Jepson (1909) and Peck (1961) accepted *P. parvifolia* as distinct from *P. hookeri* Torr. and *P. smithii* (Hook.) Utech, Shinwari & Kawano, other authors have regarded it as either a sterile hybrid between these two more widely distributed taxa (Jones 1951; Munz 1959) or as a minor variant of *P. hookeri* (McNeal 1993; Utech 2002). A recent discovery of a small population near Bear Basin Butte in Del Norte Co., California, prompted a re-examination of the taxonomic status of *P. parviflora*. Here we provide an expanded description of the species, and show that it is fertile, clearly distinct from the other five members of the genus, and probably quite rare.

TAXONOMIC STATUS

Jones (1951) regarded *Prosartes parvifolia* as a probable hybrid between *P. hookeri* and *P. smithii* because "it occurs in an area where these overlap, it is morphologically intermediate between them, and it is sterile". In contrast, Utech (2002) argued that the "the known variation in *P. hookeri* unquestionably encompasses the morphology described for *P. parvifolia*." However, *P. parvifolia* is not intermediate between *P. hookeri* and *P. smithii*, nor does it combine the traits of these two species in the mosaic-like fashion expected of a later-generation recombinant (Figs. 1, 2; Table 1; see next section). Moreover, flowers produce well-formed, apparently viable pollen, and although the ovaries of some flowers are abortive, we have observed fruits with fully filled seeds as well as seedlings at several sites. Thus, a hybrid origin seems unlikely. Although *P. parvifolia* resembles *P. hookeri* vegetatively, the two species differ consistently for several qualitative characters (Fig. 2, Table 1). In addition, they are sympatric at several sites without intergradation.

FLORAL MORPHOLOGY, POLLINATION BIOLOGY, AND RELATIONSHIPS

Prosartes parvifolia differs from other *Prosartes* in floral morphology and pollinator reward. Species in the genus form three groups based on floral plan. (1) *P. hookeri*, *P. languinosa* (Michx.) D. Don, *P. maculata* (Buckley) A. Gray, and *P. trachycarpa* S. Watson have more-or-less spreading tepals comprising a turbinate to open perianth and long filaments with exposed anthers well separated from the style and stigma (Fig. 2D). The base of each tepal is nectariferous and deeply concave. (2) The tepals of *P. smithii* likewise produce nectar at their concave bases, but the tepals are erect and reflexed only at the tip, forming a more-or-less cylindrical perianth with a narrow opening. The erect filaments position the anthers inside the perianth tube just below the stigmas (Fig. 2G). (3) The tepals of *P. parvifolia* form a campanulate perianth (Fig. 2A). In contrast to the other five species, the tepals are not strongly concave at the base, and do not produce nectar. The bases are flat or shallowly concave with a lustrous green patch contrasting sharply with the white perianth. The filaments are short and erect, and the anthers form a loose cone around the base of the style, well below the stigma (Fig. 2B). The anthers are introrse.

In northern California, flowers of *P. hookeri* and *P. smithii* are pollinated by bees (mainly *Bombus*) which probe tepal bases for nectar and

FIG. 1. Habit of *Prosartes parvifolia*. French Hill Road, Del Norte Co., California.

collect pollen either passively or actively (Mesler personal observations). Although the shiny green tepal patches of *P. parvifolia* resemble nectaries, the flowers offer only pollen as reward. On three separate occasions (in different populations), we witnessed bumblebees buzz pollen from the anther cone as in sympatric Ericaceae (*Gaultheria shallon* Pursh, *G. ovatifolia* A. Gray, *Vaccinium ovatum* Pursh) (Mesler personal observations).

Prosartes parvifolia differs most strongly from other *Prosartes* species in gynoecial morphology. The ovary has a single locule (not three) that produces 1 to 4 ovules (usually 2), which are attached near the base of a parietal placenta. The ovules are held erect so that the raphe lies next to the placenta and the micropyle faces down (hypotropous-ventral; see Simpson 2006, Fig. 11.14). In contrast the ovules of *P. hookeri* and *P. smithii* are pendent from the top of an axile placenta; the raphe faces the placenta but the micropyle points up (epitropous-ventral). The ovules of *P. lanuginosa* appear to be likewise epitropous-ventral. The ovules of *P. trachycarpa* and *P. maculata* have been described as horizontal (Jones 1951; Utech 2002), with the micropyle below the funiculus (Jones 1951). An alteration in orientation (horizontal to erect) could convert such a pleurotropous-dorsal organization to the hypotropous-ventral plan seen in *P. parvifolia* (Simpson 2006, Fig. 11.14). The fact that the

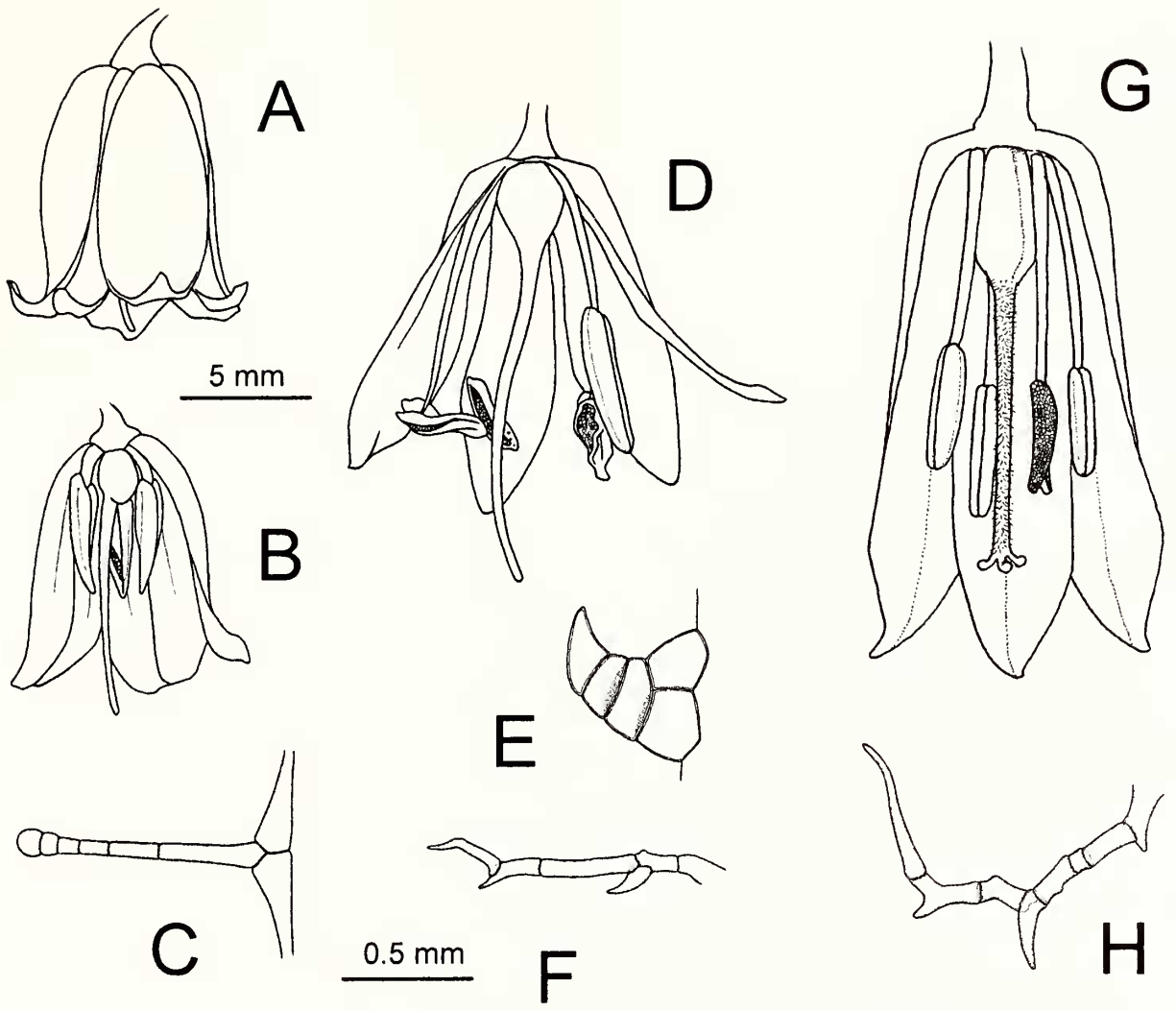

FIG. 2. Comparison of *Prosartes parvifolia* (A–C), *P. hookeri* (D–F), and *P. smithii* (G and H). A, B: intact flower and flower dissection. C: glandular hair from leaf margin. D: flower dissection. E: hair from leaf margin. F: hair from upper stem. G: flower dissection. H: hair from upper stem. Hairs and flowers are shown at the same scale.

ovaries of *P. parvifolia* are relatively small and even abortive in some flowers, coupled with routine fruit abortion, probably contributed to the conclusion of some authors (e.g., Abrams 1923; Jones 1951; Munz 1959) that the species is completely sterile.

The fleshy fruits of *P. parvifolia* typically produce two seeds, unlike other species in genus, which (except for *P. lanuginosa*) usually produce at least one seed per ovary locule (Jones 1951; Utech 2002). Developing fruits are strongly asymmetrical and remain slightly so at maturity, with the stylar scar offset from the tip. This asymmetry in conjunction with parietal (vs. central or basal) placentation suggests that the unilocular condition of *P. parvifolia* has resulted from suppression of two of the three original locules as opposed to the loss of septa to form a common chamber. Detailed anatomical and developmental studies will be needed to verify this interpretation.

The strongly divergent floral traits of *P. parvifolia* make it difficult to assess its relationships to other members of the genus, but there is currently no reason to suspect a close affinity with *P. hookeri*, the prior taxonomic connection between the two taxa notwithstanding. The orientation of ovules of *P. maculata* and *P. trachycarpa* and their glandular trichomes provide some hint of relationship with *P. parvifolia*, but resolution of the issue awaits molecular phylogenetic study and determination of chromosome number.

KEY TO PROSARTES OF NORTHWESTERN CALIFORNIA AND SOUTHWESTERN OREGON

The following key allows reliable separation of *Prosartes hookeri*, *P. parvifolia*, and *P. smithii* in northern California and southwestern Oregon. Vestiture traits are especially useful in the field because the diagnostic glandular hairs of *P. parvifolia* are seen easily on both juveniles and adults, and they persist throughout the season. However, these hairs shrink and twist upon drying, making their glandular character obscure on herbarium specimens.

1a. Leaf margins, stems, and pedicels with glandular hairs; filaments <1 mm, much shorter than dehisced anthers; fruits generally with 2 seeds, style scar offset from the apex . . . . . *Prosartes parvifolia*

1b. Leaf margins, stems, and pedicels hairy or not, but lacking glandular hairs; filaments >3 mm, longer than dehisced anthers; fruits generally with >3 seeds, style scar centered at the apex

2a. Leaf margins with numerous short, sharp, forward-pointing hairs; lower blade sur-

TABLE 1. COMPARISON OF *PROSARTES HOOKERI*, *P. PARVIFOLIA*, AND *P. SMITHII*. Based partly on Jones (1951), McNeal (1993), and Utech (2002).

	P. hookeri	*P. parvifolia*	*P. smithii*
Vestiture			
Stem	simple or branched sharp hairs (Fig. 2F)	mix of slender simple glandular hairs + shorter, eglandular clavate hairs	branched sharp hairs (Fig. 2H)
Leaf surfaces	both surfaces scabrous, with numerous short, simple sharp hairs	both surfaces smooth, with simple glandular hairs	both surfaces smooth, upper surface glabrous, lower surface glabrous or with short simple or branched hairs
Leaf margin	short, forward-pointing hairs (Fig. 2E)	slender, spreading, glandular hairs (Fig. 2C)	glabrous or with slender, spreading, simple or branched sharp hairs
Perianth shape	turbinate, tepals spreading from the middle, base narrowed, obtuse	campanulate to narrowly campanulate, tepals recurved at tip, base tapered, acute to obtuse	cylindrical, tepals closely appressed, spreading slightly at tip to form narrow opening, base truncate
Tepals			
Color	pale-green, yellow-green, or white	bright white	cream-white to white
Shape	oblanceolate to elliptical, lower 1/3 to 1/2 deeply folded along midvein	elliptical, base weakly gibbous	oblong-lanceolate, lower 1/5 to 1/4 deeply folded along midvein
Androecium			
Filament orientation and anther position (post-dehiscence)	spreading, anthers held away from style, gen exserted or +/− equal to tepals	erect, anthers included, loosely connivent around lower half of style	erect, anthers included, surrounding upper part of style, immediately below stigma lobes
Filament length	>5 mm, longer than anthers, generally unequal at dehiscence	<1 mm, much shorter than anthers, equal	>5 mm, longer than anthers, equal
Anther shape	oblong to lanceolate, apex tapered with a short, blunt mucro	lanceolate, apex narrowly acute	oblong, apex blunt or notched
Dehiscence	latrorse, anther walls folded back at maturity, often twisted	introrse, anther walls not folded back	latrorse, anther walls folded back
Gynoecium			
Style	exserted or +/− equal to tepals, 3 minute lobes surrounding central depression at apex	exserted or +/− equal to tepals, unlobed, obscurely cleft on one side at apex	included, 3-lobed, each lobe with an obscure adaxial cleft
Ovary x.s.	weakly triangular, vertices rounded	+/− terete to slightly flattened	triangular, vertices acute
Locule number	3	1	3
Ovule number	2/locule	2 (3, 4) [total]	gen >2/locule
Ovule orientation	pendent from top of placenta, micropyle facing up	erect from base of placenta, micropyle facing down	pendent from top half of placenta, micropyle facing up
Pollinator reward	nectar and pollen	pollen only	nectar and pollen
Fruits			
Color	red to orange-red	orange-red	orange to orange-red
x.s. shape	+/− terete	slightly flattened	+/− terete
Position of stylar scar	at tip	offset from tip	at tip
Chromosome number	2n = 18	not known	2n = 16
Geography	widely distributed in the mountains of the Pacific Northwest to the Rockies (disjunct in Michigan), 100–2000 m	probably rare, limited to the Siskiyou Mountains of Del Norte Co., California, and Curry and Josephine Cos., Oregon, 600 to 1525 m	common near the coast, from the San Francisco Bay area to British Columbia, 0–1500 m

face scabrous; stigma unlobed . . . . . *Prosartes hookeri*

2b. Leaf margins glabrous or with slender spreading hairs; lower blade surface smooth; stigma three-lobed . . . *Prosartes smithii*

Revised Description

Prosartes parvifolia S. Watson, Botany of California 2:179. 1880. *Disporum parvifolium* (S. Watson) Torrey. 1888. Bull. Torrey Bot. Club 15: 188.—Type: USA, California, Del Norte Co., between Happy Camp and Waldo, 16 June 1879, *V. Rattan s.n.* (holotype: GH 30030!; isotype: DS 49627!).

Plants 10–75 cm tall, sometimes clumped, from deeply buried, often vertically oriented rhizomes; flowering individuals with 1 to several aerial shoots, each with 1 to 9 spreading (shade) to strongly ascending (sun) main branches, these branched 0 to 4 times. **Stems** densely glandular pubescent, with slender multicellular glandular hairs and shorter, eglandular, clavate hairs; base of stem with 2–4 densely pubescent cataphyll bracts, these sometimes subtending the first or second main branch. Foliage **leaves** sessile; blade broadly ovate to lance-ovate, less often lance-oblong or elliptic, flat (shade) or strongly folded (sun), 1.8–5.3 cm long, 0.6–3.4 cm wide; apex acute to acuminate, base rounded to cordate, symmetrical to slightly oblique, often +/− clasping (especially when subtending major branches), both surfaces with slender, erect multicellular glandular hairs especially along veins; margins flat or undulate (sun), with slender, spreading, multicellular, glandular hairs. **Inflorescences** with 1–4 flowers; pedicels 4–10 mm long, densely pubescent, with multicellular glandular hairs. **Flowers** 8–10 mm long, 6–8 mm wide, pendent, bright white, campanulate to narrowly campanulate; base of perianth tapered; tepals elliptical, broadly concave, apex recurved, acute, base weakly gibbous, shallowly concave abaxially or +/− flat, with a rounded or quadrate shiny dark green patch; outer tepals 9–10 mm long, 3–5 mm wide; inner tepals 9–10 mm long, 2–4 mm wide; stamens subsessile, +/− erect, forming a loose cone around the style; filaments short and broad, 0.4–0.8 mm long, 0.4 mm wide; anthers lanceolate, introrse, basifixed, 3.6–4.3 mm long, 0.8 mm wide, apex narrowly acute, base sagittate; pollen white; style 8–10 mm long, sparsely pubescent or glabrous at base, not centered on apex of ovary, slightly curved, exserted ≤1 mm or slightly included, tip very obscurely cleft on one side; ovary small (sometimes abortive), pubescent to sparsely pubescent at top, 0.9–1.0 mm long, 0.7–1.0 mm wide, weakly angled, asymmetrical (flat or grooved on one side, convex on the other), with one locule and 2 (3) ovules; placenta parietal; ovules erect, hypotropous-ventral. **Fruits** fleshy, orange to orange-red, slightly flattened, not expanded equally around pedicel-style axis; stylar scar displaced to one side of apex, 10–13 mm long, 8–10 mm wide; seeds (1) 2 (3), white, 5.5–6.5 mm long when fresh.

Specimens Examined

CALIFORNIA. **Del Norte Co.**: E base of Hazelview Summit grade, 19 May 1929, *D. Kildale 7874* (CAS); Hazelview Summit, 25 May 1929, *D. Kildale 9176* (CAS); French Hill Road, 21.6 mi from intersection with Hwy 199, cut-over Douglas Fir forest, 30 June 1970, *J. P. Smith and S. Silva 4254* (HSC); Near Bear Basin, herb layer of evergreen conifer forest, 41°48′21.7″, 123°44′11.1″, 22 June 1979, *G. L. Clifton and T. Griswold 5670* (HSC); T17N, R3E, sec 25, FS road 17N05, 1.5 mi N of road 17N04, UTM 435423 E, 4632830 N (NAD 27), elev. 1005 m (3300 ft), steep roadside below *Lithocarpus* and *Pseudotsuga*, 11 June 2006, *M. R. Mesler 615* (HSC); T17N R4E, sec 32, UTM 437032E, 4629798N (NAD 27), along unlabeled logging spur of FS road 17N05, 1.0 mi from intersection with FS road 17N04, about 100 m from the main road, elev. 1067 m (4000 ft), on edge of road and under *Pseudotsuga* and *Chrysolepis*, 10 June 2007, *M. R. Mesler 762* (HSC); T16N, R4E, sec 4, UTM 437109 E, 4629757 N (NAD 27), FS road 16N02, 40 paces beyond spur to Bear Basin Lookout, below road, elev. 1524 m (5000 ft), understory of *Abies concolor*/*Abies magnifica* forest, 29 June 2006, *M. R. Mesler 623* (HSC); T18N, R3E, sec 1, UTM 434606 E, 4648843 N (NAD 27), elev. 945 m (3100 ft), logging spur running S from FS 4402, 0.1 mi E of county road 316, exposed roadside, 9 September 2006, *M. R. Mesler 633* (HSC); UTM 434606 E, 4648843 N (NAD 27), elev. 945 m (3100 ft), logging road running S of FS 4402, 0.1 mile E of intersection with road 316. 1 September 2006, *Mesler 634* (HSC); T18N, R4E, sec. 9, UTM 438620 E, 4646536 N (NAD 27), elev. 700 m (2300 ft), county road 324, 4.4 mi from its western intersection with Hwy 199, E of Hazelview Summit, 17 May 2007, *Mesler 755* (HSC); 41.826°N, 123.929°W, elev. 733 m (2404 ft), French Hill Road, 7.4 mi from Hwy 199, 29 May 2008, *M. Simpson 3028* (HSC). OREGON. **Curry Co.**: Coast Mountains, 42nd parallel, 13 June 1884, *T. J. Howell* (OSU); Bear Wallow Lookout, 4 June 1932, *L. Leach 3548* (OSU); T40S, R11W, sec 9, UTM 416824 E, 4660822 N (NAD 27), elev. 580 m (1900 ft), at the end of road 330, running S from FS road 1107, 0.8 mi SE of intersection with road 334, 1 September 2006, *M. Mesler 636* (HSC); T40S, R10W, sec. 24, UTM 431559 E, 4657932 N (NAD 27), elev. 1100 m (3600 ft), Buckskin Peak trail, 14 September 2007, *M. Mesler 789* (HSC). **Josephine**

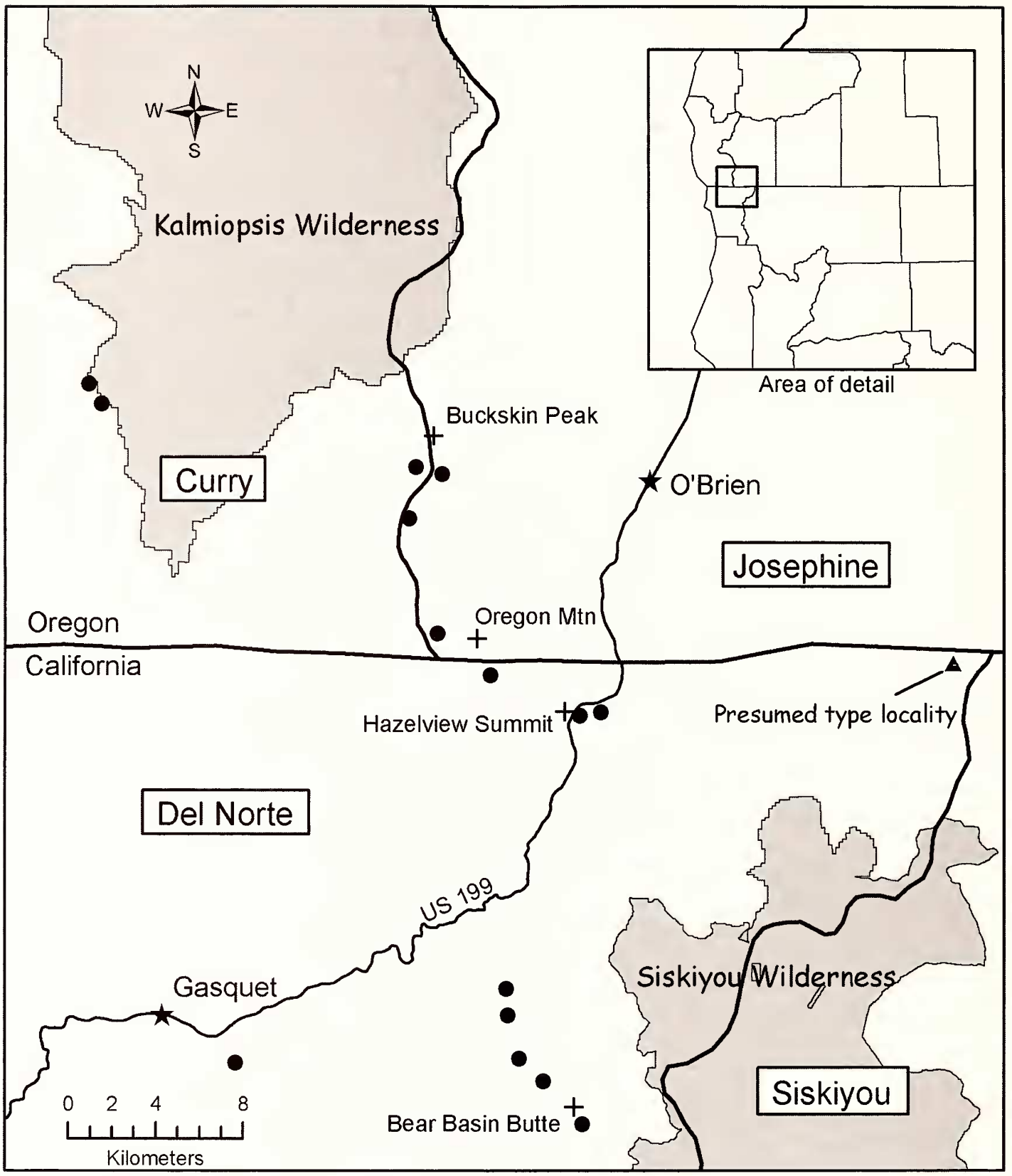

FIG. 3. Distribution of *Prosartes parvifolia*. Points are currently known populations; the diamond shows the estimated position of the type locality.

Co.: Hunter's Camp, between Chetco Ridge trail and Rough and Ready trail, 26 June 1950, *A. Kruckeberg 1972* (OSU); T41S, R10W, sec. 13, UTM 431469 E, 4650295 N (NAD 27), elev. 1070 m (3500 ft), Wimer Rd (FS 4402), 1.0 mi E of intersection of 4402 and 4402.112, 14 September 2007, *M. Mesler 790* (HSC).

DISTRIBUTION AND HABITAT

Prosartes parvifolia is confined almost entirely to the Smith River watershed of the Siskiyou Mountains of northwestern California and southwestern Oregon (Del Norte, Curry, and Josephine counties; Fig. 3). Exceptions are two populations east of the Kalmiopsis Wilderness (Coast Ranges) and one near Buckskin Peak (Illinois River watershed). A putative population, identified by G. J. Muth in 1978 (Flora of Klamath Mountains, unpublished computer-generated checklist, Pacific Union College, Angwin, CA) and located near El Capitan in Siskiyou Co. (*Butler 00026* [PUA]) is *P. hookeri*.

Plants grow on various metamorphic substrates (not ultramafic soils) in shaded forest understories and forest edges as well as on adjacent exposed roadside slopes and at logged and burned sites, at elevations from 600 to

1525 m. The most common tree associate is *Pseudotsuga menziesii* (Mirb.) Franco, occurring in combination with *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon, & S. Oh at lower elevations and *Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr. var. *lowiana* (Gordon & Glend.) Lemmon and *A. magnifica* A. Murray at higher elevations. Other common associates are *Chrysolepis chrysophylla* (Douglas ex Hook.) Hjelmq., *Gaultheria shallon* Pursh, *G. ovatifolia* A. Gray, *Mahonia repens* (Lindl.) G. Don, *Quercus sadleriana* R. Br. ter, and *Rhododendron macrophyllum* D. Don ex G. Don.

History of Collection and Rarity

Prior to our study, *Prosartes parvifolia* had been collected only eight times. The type collection was made by Volney Rattan in 1879 along the road connecting Happy Camp, California, and Waldo, Oregon. The species was collected five years later by Thomas Howell, probably in the same general area, and then again by Lilla Leach and Doris Kildale Niles in 1929 and 1932, respectively. Each of these inveterate explorers of the Siskiyou Mountains collected the species from just a single locality or pair of closely spaced localities. The most recent collection was made near Oregon Mountain in 1998 by Veva Stansell, who reports having encountered it only once over many years of exploration (local botanist, personal communication).

Prosartes parvifolia qualifies as rare, at least by virtue of its very narrow geographical distribution. Currently it is known from only 15 locations spread over an area of about 525 km^2; the most distant pair of sites is separated by only 40 km (Fig. 3). We have re-discovered all of the historical collection areas with the exception of the type locality and a site visited by Kruckeberg in 1950 (see Specimens Examined, Josephine Co., OR) on the east side of the Kalmiopsis Wilderness that probably lies slightly north of populations we found near Buckskin Peak. Based on field reconnaissance in 2006–2009, we estimate fewer than 500 reproductive-age individuals across the 15 known sites. Our estimates may be conservative since a good deal of the roadless, rugged terrain in the Siskyou/Klamath region remains poorly explored botanically (J. Sawyer, Humboldt State Univ., personal communication). Nevertheless, if such a distinctive taxon were truly abundant, we believe the many avid botanists who have worked in the area would have encountered it much more commonly.

The factors responsible for the apparent rarity of *P. parvifolia* are unknown. The species is not a strong habitat specialist. It occurs across a wide range of elevations on a variety of relatively productive substrates in association with varying mixes of trees, in both shade and sun. The same habitat settings are common throughout the Klamath and adjoining Coast Range Mountains. Logging and road construction may have contributed to population declines, but the paucity of early collections suggests that the species may have been rare historically. The largest, most floriferous plants grow on otherwise bare mineral substrate along road cuts, and the largest known population occupies a recently cut and burned Douglas fir forest. Pollination deficits might be expected given small population sizes, but we have found isolated individuals with heavy fruit crops. The major threats facing *P. parvifolia* appear to be its limited distribution and small population sizes.

Acknowledgments

We thank Veva Stansell, John Sawyer, Erik Jules, Jen Kalt, Jenny Nyffeneger, James P. Smith, Gibby Muth, Steve Darington, an anonymous reviewer, Lola Bell and Violet for encouragement, information, help in the field and lab, and/or comments on the manuscript. We are indebted to the curators of the following herbaria for loans: CAS, OSU, and WU. We dedicate this paper to the early plant explorers who first collected Siskiyou Bells and, especially, to our good friend, John Sawyer, whose unparalleled knowledge of the Klamath Region and passion for field work has been an inspiration.

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